Contents

CEH research programmes

Biodiversity, the natural biological capital of the earth, embraces genetic diversity, species diversity and ecosystem diversity – three major levels of organisation in the natural world. As such, its preservation and wise utilisation are intimately linked to the healthy functioning of natural and semi-natural ecosystems, to the quality of life, and to wealth creation.

Biodiversity

Through the Convention on Biological Diversity and a diverse range of global and European protocols and legislation, the UK Government is committed to the conservation and sustainable use of biodiversity. In accordance with the high priority now given to this subject, one of NERC's six environmental and natural resource issues within the new funding model – which defines the focus of its thematic and core strategic programmes – is dedicated to biodiversity.

Historically, much research into biodiversity has been done in the UK and the national biodiversity research effort has developed a number of broad characteristics. First, there are many nationwide monitoring schemes that provide an invaluable source of data for exploring spatial patterns in diversity at the geographic scale. Second, much research emphasis is placed on wetlands because, as a signatory to the Ramsar Convention on Wetlands of International Importance, the UK Government is 'obliged to ensure wise use and conservation of their wetlands because of their abundant richness in flora and fauna and their economically important functions and values'. Third, there is a strong multi-national, increasingly tropical, dimension.

All these three features characterise the developing biodiversity research programme in CEH. There are five strategic objectives which follow from the national obligations and NERC's commitment to them.

- We need to describe and measure biodiversity, to monitor changes in diversity and to identify associations between diversity and environmental factors, over both time and space. This objective is concerned with defining our biodiversity capital and in establishing patterns of variation and change.
- We must understand the reciprocal interactions between biodiversity and the functioning of ecosystems. This is concerned with investigating processes explicitly involved in the evolution and maintenance of diversity.
- The patterns of diversity and the processes that cause them depend on the responses of species populations to other species and to their common environment. An understanding of the population ecology of single species, and of groups of interacting species, therefore provides the essential basis for understanding biodiversity and for predicting its

response to environmental change
- Based on the understanding acquired by pursuing these three objectives, we can explore how best to conserve and to exploit biodiversity sustainably for man's immediate benefit, without diminishing its value to future generations
- But, as mistakes have already been made, and will continue to be made, we should finally ask how we can best restore biodiversity where it has already been damaged or destroyed

This research programme has been set up to investigate biodiversity and the fundamental population processes upon which it depends Each of its five projects corresponds with one of the five strategic objectives

Biodiversity characterisation, pattern and monitoring is concerned with the traditional initial stage in science of describing the phenomenon and identifying patterns, in both space and time, which might give insights into the underlying processes that determine pattern An example of ITE's role in this project is using the Biological Records Centre data to relate biodiversity to environmental gradients in space and to environmental changes over time

Ecosystem function and biodiversity embraces the normal second phase in science of investigating the processes by which patterns have been created and maintained It is concerned with the evolution of biodiversity and the processes within ecosystems that maintain diversity at all levels of organisation, and with the role, in turn, that biodiversity plays in the functioning and presistence of ecosystems An example of research in this project is provided by Ward, Clarke and Hackshaw Their aim is to understand the evolutionary background to the highly specific food plant preferences of the many thousands of plant-feeding insects that occur in the UK This specificity is caused by plant chemicals that enable insects to recognise their food plants and so avoid the noxious compounds that plants use to defend themselves against defoliation The evolution of deterrent chemistry has greatly affected the numbers of insect species that can live on each plant species and thus has had a direct influence on biodiversity

Population processes underlying biodiversity focuses on the reciprocal interactions between species, and between species and their environment, and may often involve the study of genetic aspects of population ecology An understanding of population processes is vital to provide explanations of, and a predictive framework for, how biodiversity is created and maintained The reports by Moss and Bacon and by Stillman and Goss-Custard both contribute to this project as, in their different ways, they deal with the population processes that underlie biodiversity The authors use mathematical models so that they can express their understanding of their study populations quantitatively and make precise predictions for testing in the field

The models of Moss and Bacon and of Stillman and Goss-Custard also give predictions as to how populations will respond to environmental change and to alternative land management policies In the cases of Moss and Bacon, the study species is itself exploited by man In the case of Stillman, the study species competes with people for shellfish Both of these studies illustrate how curiosity-driven research in the first three projects contributes directly to achieving the largely applied objectives of the other two projects in the biodiversity programme

Conservation and sustainable use of biodiversity aims to improve our ability to conserve biodiversity while, in many systems, exploiting it for the long-term benefit of people

Restoration of biodiversity also applies the principles established under the first three projects, in this case to re-establish diversity where it has been lost As an example, the work of Bullock, Hodder and Manchester is concerned with assessing the positive and negative environmental impacts of translocating single species and whole communities of species from one place to another They aim to develop techniques that will allow the early detection and control of environmental problems caused by translocations and improve the environmental gains from translocations carried out for conservation purposes

Restoration ecology is expected to be a major growth area in ITE It provides exciting possibilities for applying research findings to practical problems and opportunities to conduct large-scale ecological experiments for testing further our understanding of ecological systems As in all the projects in the biodiversity programme, the research is designed to provide the strategic underpinning science from which policy-makers will be able to draw the best possible guidance as to how they can combine the UK Government's objective of increasing wealth creation from biodiversity while maintaining its value as a major contributor towards the quality of life

J D Goss-Custard and A J Gray

Plate 8. Most phytophagous insects feed on a limited range of plants
i. Juniper shield bug (Acanthosomatidae) feeds on berries of juniper and introduced Cupressaceae
ii. High brown fritillary butterfly caterpillars (Nymphalidae) feed on violets (Violaceae)
iii. Asparagus beetle (Chrysomelidae) larvae feed on species of asparagus (Liliaceae)
iv. *Stigmella* sp. (Nepticulidae) mine in leaves of blackberry and a few other Rosaceae

Evolution of insects and their plant hosts

Insect food plant records for 6935 species of insects and about 2000 plants in Britain have been collated for the Phytophagous Insects Data Bank (PIDB). The validity and interpretation of these records were discussed by Ward (1988). Currently, the data are being analysed to understand the evolutionary background, as part of the explanation of insect food plant preferences that are observed today.

Most plant-feeding insects feed on a limited number of plant species; some examples are shown in Plate 8. In the PIDB records, 75.8% of the species were restricted to one plant family (Ward & Spalding 1993). Specificity does vary within insect families. Those with very close relationships to plants, eg galling, or mining internally in leaves, have species that are very specific. Others, such as the large caterpillars of noctuid moths, have nearly half of their species polyphagous (Table 7). Host switching has occurred in the ancient past, and still occurs, but is more limited when food plants are in entirely unrelated families. This spectrum of plant families on which each family of insects feeds has been analysed to show the overall patterns of preferences for plants.

Relationships between insect and plant families

The relationships and similarities between the 117 plant families and the 182 phytophagous insect/mite families occurring on them were represented by the use of a multivariate statistical technique called 'correspondence analysis'. This technique gives each of the plant families and insect families scores along one or more ordination axes, such that on any one axis the score of a plant family is the weighted average of the scores of the insect families which feed on that particular plant family. Similarly, the ordination score of an insect family is the weighted average of the scores of the plant families on which it feeds, hence the alternative name for the technique of 'reciprocal averaging'. The scores are calculated in order to explain as much of the variation as possible between the plant families in relation to their insect composition. (Technically, this can be thought of as maximising the variance of the plant family scores relative to the average variance in plant family host scores within each insect family.) The data for this analysis consisted of the numbers of insect species (used as weights) within an insect family which fed on a particular plant family. The relationships between plants and insects are shown using bivariate plots of the first two ordination axes, which acount for the most variation over all axes. Insect families and plant families which are close together on the bi-plot indicate a tendency to be associated with each other; ie those insects tend to be most commonly found on those types of plants.

The first two axes explain 15.1% of the total variance, a reasonable and typical proportion given the number of plant families and insect groups involved and the complexity of biological mechanisms causing the associations.

Evolutionary significance

The patterning of the results for insect and plant families together show at least two gradients (Figure 23 – some plant families labelled). One gradient is from conifers and trees through shrubs and subshrubs to herbaceous dicots. These life forms of plants are important evolutionary centres for radiations of species and host switching (Ward, Hackshaw & Clarke 1995), but they may also be representing past plant evolution. Plants which evolved in earlier geological epochs, such as conifers (Triassic and Jurassic) and some woody dicot trees (Cretaceous), can be regarded as more 'primitive'. These families appear in the lower part of Figure 23. Most of the herbs evolved later, and are placed in the upper part of Figure 23. A second gradient appears to be of increasingly aquatic herbs, with a group of the monocotyledenous grasses, sedges and rushes on the left.

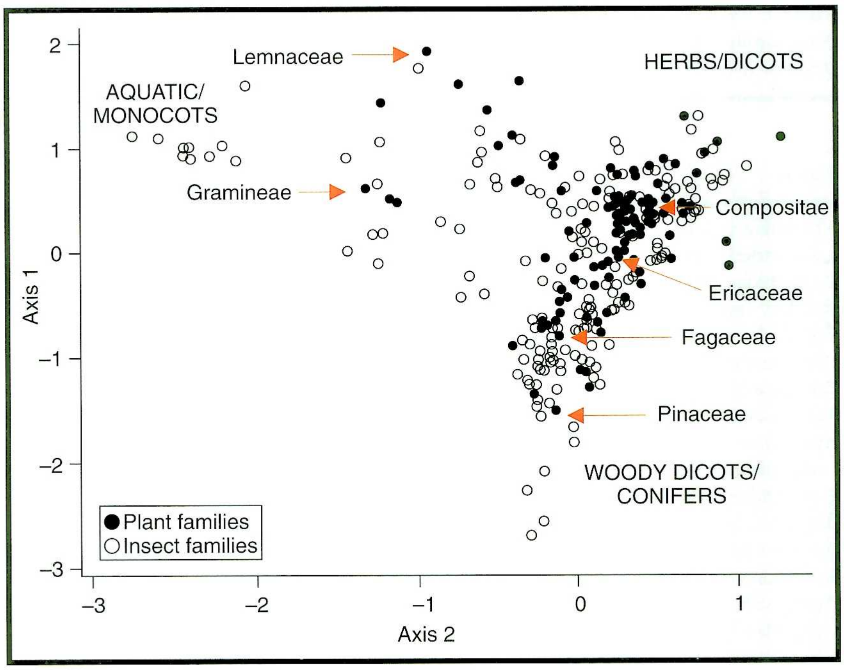

Figure 23. All families of plants and insects in the correspondence analysis (main habitat/taxa groups are shown although there is some variation in details: some plant families labelled)

All the major orders of insects have phytophagous species, but it is impractical to show all these families in this report; therefore, the contrast between Hymenoptera (sawflies, gall wasps) and Diptera (two-winged flies) is illustrated by data extracted for Figure 24. Some important families are labelled.

All the major orders of insects have phytophagous species.

Hymenoptera are represented principally by sawflies, an ancient group of insects mainly associated with woody plants. Fossils of the primitive small family, Xyelidae, were recorded as long ago as the Triassic. Almost all Hymenopterous families are in the lower half of Figure 24. Xyelidae, with the lowest value on Axis 1, is associated with conifers in Britain, as are most of the world species. The largest family of sawflies, Tenthredinidae, with tribes ranging from primitive to advanced, is fairly central in Figure 24. Eurytomidae, however, are a later-evolved group of parasitic wasps, where some species have become phytophagous, causing simple galls on Gramineae (grasses).

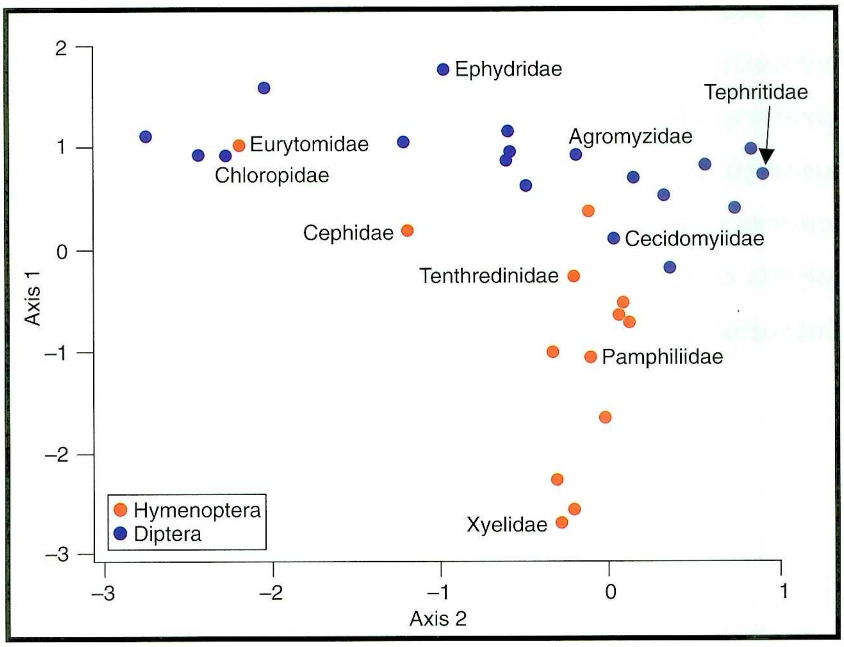

Figure 24. Families of plant-feeding Hymenoptera (sawflies, galls wasps, etc) and Diptera (gall midges, gall flies, agromyzid mining flies, etc) in the correspondence analysis (some families labelled)

Table 7 Percentage of polyphagous insect species and percentage feeding on only one plant family for large insect families in Britain (polyphagous species defined feeding on three or more plant families or noted by the author of the record as polyphagous)

Family	Percentage Polyphagous	 Only on one plant family	Total phytophagous species in insect family in GB
Noctuidae (noctuid moths)	47 0	45 7	383
Geometridae (geometrid moths)	39 5	44 6	294
Cicadellidae (leafhoppers)	28 1	59 8	249
Miridae* (mirid bugs)	27 1	65 2	181
Tortricidae (tortricid moths)	22 7	70 0	313
Chrysomelidae (leaf beetles)	22 4	57 3	255
Curculionidae (curculionid weevils)	13 1	73 8	366
Tenthredinidae (tenthredinid sawflies)	9 8	79 1	377
Aphididae+ (aphids)	9 2	87 6	467
Coleophoridae (case-bearing micro-moths)	5 7	88 7	106
Gelechiidae (gelechid micro-moths)	3 5	92 4	145
Agromyzidae (agromyzid mining flies)	2 0	94 7	301
Eriophyidae (eriophyid mites)	0 9	93 4	228
Cecidomyiidae (gall midges)	0 2	98 9	443
Nepticulidae (nepticulid micro-moths)	0 0	98 0	98
Cynipidae (gall wasps)	0 0	98 6	72
TOTAL in database	15 2	75 8	6933

* 51 partly predacious + winter and summer morphs counted as separate 'species'

Gramineae is an advanced family of plants (Cronquist 1981), and the associated Eurytomidae are placed highest of the Hymenoptera in the analysis

Diptera are a later-evolved order of insects than Hymenoptera and are associated with herbs, particularly Gramineae and Compositae (a large later-evolved family) Families of Diptera are almost all placed higher than Hymenoptera on axis 1 (Figure 24) Cecidomyiidae (gall midges), in the less advanced sub-order Nematocera, are placed lower than the majority of Diptera The 443 species of Cecidomyiidae recorded have strong associations with Papilionaceae (vetches), although many other plants are attacked Advanced Cyclorrhapha, like Tephritidae (gall flies) and Agromyzidae, are commonest on Compositae, while phytophagous Ephydridae feed on aquatic plants

The study of the evolution of food plant preferences by insects is used to predict the likely course of events when plants or insects are introduced to new areas.

Conclusion

The study of the evolution of food plant preferences by insects is intrinsically interesting, but has other applications, eg to predict the likely course of events when plants or insects are introduced to new areas This is mediated by the chemical features which enable insects to recognise their food plants, and the broad features of deterrent chemistry will be included in a more detailed paper on the evolution of insects and their food plants

L K Ward, R T Clarke and A Hackshaw

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Plate 9. Cock red grouse

Red grouse population modelling

Complex patterns produced from simple deterministic processes provide intriguing insight into many physical and biological phenomena. In some single-species population models, changes in population size may be regular cycles or chaotic fluctuations which are unpredictable and highly sensitive to initial conditions. Population biologists interested in patterns of animal and plant abundance are trying to characterise dynamics and detect chaos by analysing patterns of change in population size. However, theory shows that regular cycles and chaos may be produced by the same underlying processes, and that regular cycles are easier to detect than chaos. This possibility gives fresh interest to one of the longest-standing enigmas in population biology: the cyclic changes in numbers that occur in small vertebrates (voles, lemmings, hares and birds of the grouse family) in northern latitudes.

Traditional explanations of population cycles are often based on the idea of negative feedback between population density and growth. Cycles may occur if the feedback occurs with a delay, or lag (Turchin & Taylor 1992). The idea is homologous with oscillations due to 'hunting' in mechanical or physiological systems. For example, cycles can be generated when an increase or decrease in the abundance of prey is followed one year later by an increase or decrease in the abundance of the predator that feeds on it. The population growth rate of the exploiter lags behind that of the exploited so that, for example, prey numbers can increase rapidly before the predator population can increase and exert downward pressure on prey numbers. However, one does not need to invoke another species and, more parsimoniously, can postulate that cycles result simply from the intrinsic demographic equations governing population growth within a species.

The form of these demographic functions will, of course, depend on the biological processes underlying them. We need to discover these processes, for understanding them is vital to providing predictions as to how populations will be affected by environmental change. In particular, it is important to know whether erratic fluctuations in numbers are always caused solely by factors external to the species themselves –

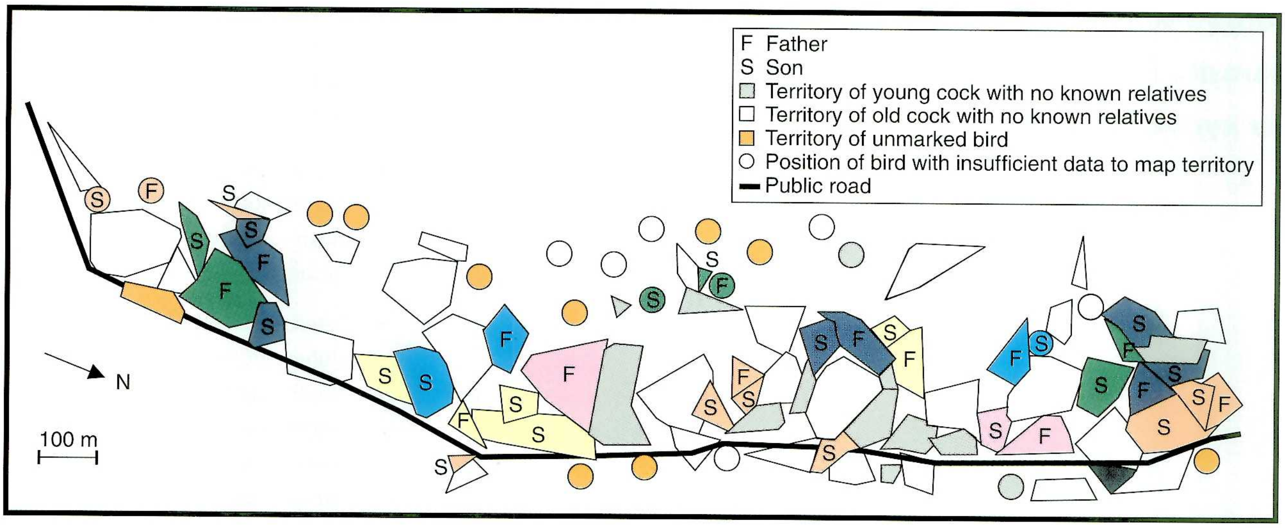

Figure 25. Red grouse territorial clusters at Glas Choille, Aberdeenshire, in autumn 1995 (source: A D C MacColl). Core territories of first-degree relatives are shown in the same colour, though widely separated clusters of the same colour are not related

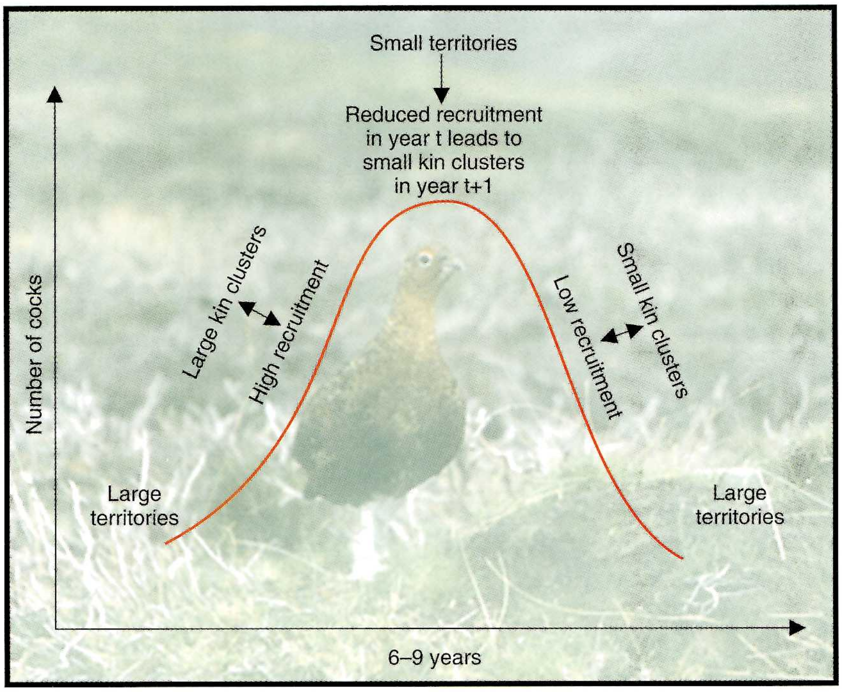

Figure 26. Outline of the processes involved in the Mountford and Matthiopoulos models of red grouse population cycles

such as predators, pathogens and food resources – or whether they can also be due to intrinsic processes such as social behaviour or genetic change. Many workers seem to agree with Stenseth and Ims (1993) that 'social and intrinsic mechanisms are unlikely to generate regular density cycles'. In our discussions with colleagues two reasons for this scepticism regularly emerge:

- first, the belief that animal numbers are largely determined by resources and natural enemies, which are 'strong' effects and likely to outweigh any 'weak' effects such as intrinsic changes in behaviour;
- second, the lack of parameterised models formalising hypotheses about intrinsic factors.

We disagree with the scepticism that intrinsic processes are unlikely to cause population cycles. With colleagues, we have recently (i) shown that experimental changes in aggressive territorial behaviour, induced by implanting testosterone beneath the skin of territorial males, caused significant changes in the population density of red grouse (*Lagopus lagopus scoticus*) (Moss, Parr & Lambin 1994), and (ii) developed models showing how changes in behaviour might cause population cycles in red grouse (Plate 9). We now focus on these models.

There is evidence from some sites that the parasite is not necessary for cycles to occur.

Behaviour and population density in red grouse

Red grouse are a subspecies of the willow ptarmigan (*Lagopus lagopus*), a monogamous, territorial bird with a circumpolar distribution. It shows cycles in much of its range, although not all populations cycle, and cycle period varies in length from three or four to ten years or more. Whilst some workers, from Dougall (1875) to Dobson and Hudson (1992), have suggested that red grouse population cycles at some locations are due to a host/parasite (grouse and caecal threadworm, *Trichostrongylus tenuis*) interaction, this can scarcely be a general explanation as the two species co-exist over only a tiny part of the bird's range. Even where they do co-exist, there is evidence from some sites that the parasite is not necessary for cycles to occur (Moss *et al.* 1993).

The hypothesis that changes in cock territorial behaviour might cause red grouse population cycles (Watson *et al.* 1994) stems from six observations.

- Red grouse numbers are limited by the territorial behaviour of cocks (Plate 10): territorial cocks and their hens survive, and breed, while non-territorial birds die.
- Changes in population density are accompanied by inverse changes in mean territory size, rather than vacant habitat.
- Territories tend to occur in philopatric family clusters (Figure 25). Father and brothers together begin their campaign of territory acquisition from the parental territory. Hence, cock offspring tend to get territories next to their fathers.

- Related individuals show less aggression to each other than to non-relatives.
- Year-to-year changes in numbers are due largely to variations in the local recruitment of young birds to the territorial population, not to changes in adult mortality.
- The proportion of contending young cocks which get territories (ie recruit) is greater in the increase than in the decline phase of cyclic fluctuations.

Models

Mean field (spatially inexplicit) models

Mountford *et al.* (1990) proposed that population cycles in red grouse are driven by the philopatric cocks and can be explained by the joint action of two factors, population density and differential behaviour between kin and non-kin (Figure 26). Recruitment is inhibited by high density: simple density dependence. The effect of kin is assumed to operate through members of territorial kin clusters facilitating the recruitment of their joint offspring: the bigger the kin cluster, the greater the proportion of offspring recruited (A D C MacColl, unpublished data). So, big kin clusters cause high recruitment which in turn gives rise to big kin clusters, resulting in positive feedback between recruitment in successive years. Increased recruitment is associated with a reduction in mean territory size which causes increased density.

The model assumes a constant background mortality due to previously territorial birds losing their territories. In order to maintain kin clusters at a given size, a certain level of recruitment is necessary. If recruitment drops below this threshold in year t, cluster size in year t+1 falls and so does recruitment. As population density increases, recruitment drops as territories approach a critical minimum size and, when it has fallen below the threshold, falling recruitment and the falling size of kin clusters cause contrary positive feedback and the population declines. As density falls, recruitment eventually increases above the threshold and the next increase begins. J Matthiopoulos, R Moss and X Lambin have now developed this model and parameterised it from field observations. It gives a reasonable account of observed population fluctuations without the need to invoke trophic interactions. Tests of its predictions are in progress.

Spatially explicit simulation

Much current work on spatially explicit versions of mean field models shows that they do not necessarily give the same results. Co-operation with R J Hendry and J M McGlade at the University of

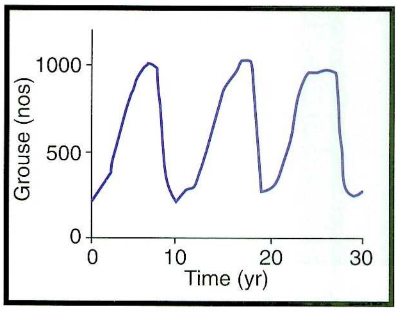

Figure 27. Population trajectory generated by the spatially explicit Hendry model of red grouse population cycles

Conditions likely to favour the evolution of unstable dynamics through territorial 'helping' behaviour

Tenet

Kin-tolerant territorial individuals are less aggressive to kin neighbours than to non-kin neighbours. This could result in them either sharing critical resources, such as territory space, or interfering less with their kin's breeding attempts than with their neighbour's. This is more likely if:

- **Resource partitioning**
  - 1 The species partitions limiting resources by, for example, defending territories (space limiting). In this case, breeding success per territory should be largely independent of territory size
- **Opportunity: recognisable kin must be available**
  - 2 Adult mortality should be high enough to allow new kin to recruit next to each other and low enough to allow local family clusters to build up
  - 3a Juvenile survival to maturity should be high enough to allow recognisable kin to settle next to each other
  - 3b Family size should be large enough to give a big pool of relatives as potential kin-recruits
- **Uniform habitat**
  - 4 This criterion reduces the possibility of population stability occurring due to dominant birds defending territories each containing a resource-rich patch
- **Group structure and alternative forms of kin co-operation**
  - 5 Kin tolerance may manifest itself in other ways, such as co-operative breeding and helping [eg scrub jays], or toleration of offspring and siblings within a group territory
  - 6 Confident recognition of kin will promote the evolution of behaviour involving kin co-operation. This is more likely if the family stays together until territories are taken up

Plate 10. Tracks made by cock red grouse patrolling their territorial boundaries in the snow

Warwick has resulted (Hendry 1996) in a spatially explicit individual-based simulation of the known processes of territory acquisition. In the initial, philopatric, phase, families gather on the paternal territory and sons attempt to take territories on its margins. In the next, dispersal, phase, sons which have so far failed to get territories move away and try again. In the absence of differential behaviour between kin and non-kin, the population reaches a stable equilibrium. Preliminary runs incorporating differential behaviour have readily generated cyclic population trajectories based on realistic assumptions and parameters (Figure 27). These simulations are computer-intensive and will require considerable time and work to explore the full parameter space properly.

Red grouse 'help' relatives to get territories and this causes unstable population dynamics.

Evolution of unstable dynamics

Our group is often asked how the situation we postulate might have evolved. The conditions outlined in the Box seem likely to favour its development. The route presumably involved a group comprising parents and offspring. Standard 'helping' in birds such as Florida scrub jays (*Aphelocoma coerulescens*), in which offspring help parents to rear young, might also have evolved through this point. We postulate that red grouse 'help' relatives to get territories and that this causes unstable population dynamics.

R Moss and P J Bacon

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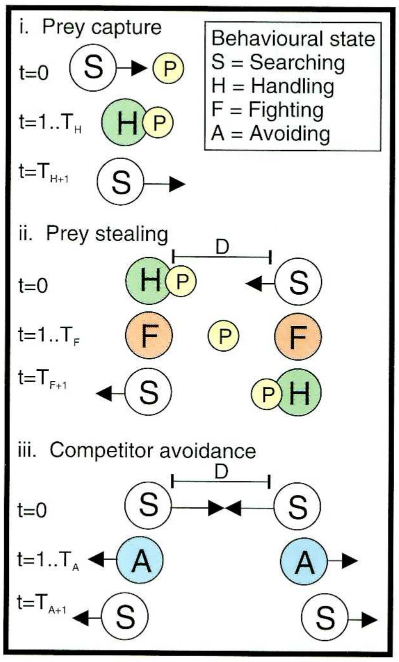

Figure 28. Methods by which foraging individuals change their behavioural state in the model (S – searching; H – handling; F – fighting; A – avoiding)
i. Prey capture – a searching animal encounters a prey (P) item, handles it for T_H seconds, consumes it, and then resumes searching
ii. Fighting over prey – a searching animal approaches another which is handling prey to within the encounter distance (D), initiates a fight over the prey which lasts for T_F seconds, after which (in this example) it wins and starts handling the prey. The victim of the attack changes direction and starts searching directly away from the aggressor
iii. Competitor avoidance – two animals approach each other to within the encounter distance (D), they both start avoiding by changing direction and moving directly away from one another for T_A seconds, after which they resume searching

Modelling behavioural interactions in shorebirds

One of the key factors thought to influence the distribution of foraging animals is the relationship between prey intake rate and the density of competitors. If competitor density does not influence intake rate, all animals should congregate in the site where intake rate is greatest. However, if interference occurs between individuals, intake rate in the best site will be reduced as the density of foragers increases. Some individuals will achieve higher intake rates in other sites, and so should spread out to a wider range of feeding locations. Measuring the strength of interference between foraging animals is therefore central to understanding their patterns of distribution.

Field studies of interference have observed animals foraging at different competitor densities, and have measured interference from the slope of the relationship between intake rate and density. Intake rate decreases at a greater rate with increasing density when interference is more intense. This approach enables interference to be quantified, but the results may only apply to the conditions under which the data were collected. For example, both food availability (Dolman 1995) and stage of the season (Stillman *et al.* 1996) may influence the strength of interference. Field studies may therefore be unreliable in predicting the strength of interference in new situations, such as when food is unusually scarce.

An alternative which has recently been developed is to use mathematical models to predict the strength of interference based on basic elements of animal behaviour, including the interactions between foraging animals (eg Holmgren 1995; Moody & Houston 1995). Basic behaviour should remain relatively constant, and so these models should produce predictions that are applicable to a wide range of conditions. Although based on very simple assumptions, these models have predicted the general form of interference relationships observed in foraging shorebirds (Stillman *et al.* 1996).

However, they have not yet been fully tested against field data, and for mathematical tractability they make a number of assumptions which are unlikely to hold for many systems. One example is that animals are assumed to have a fixed response when encountering others. In reality, their responses may depend on the likely outcomes of alternative actions; for example, an animal may attempt to steal prey from another if it expects to be successful but ignore the opportunity otherwise. In order to overcome these limitations, we are developing a simulation model, based on the mathematical theory but which includes more realistic assumptions.

The model simulates a population of animals foraging in a two-dimensional patch containing a uniform distribution of prey. Time progresses in steps of one second, during each of which each animal may be in one of four behavioural states: searching, handling, fighting or avoiding. Searching animals walk in a straight line in search of prey items which may be captured directly from the patch itself, or stolen from a competitor. On obtaining a prey item, animals enter the handling state, in which they are stationary and consume the prey. Fighting animals are

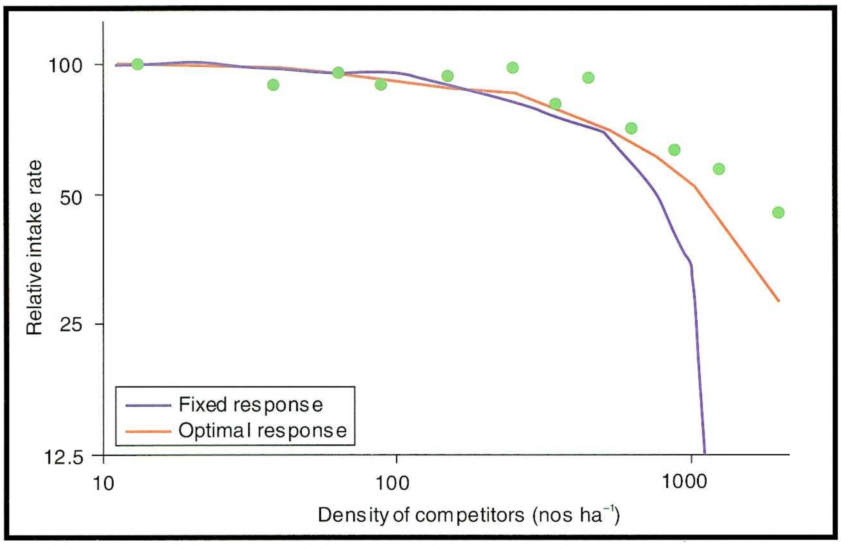

Figure 29. Test of the model predictions when either assuming that individuals always respond in the same way when encountering others (fixed response), or that they behave in order to maximise their intake rate (optimal response). The symbols show field results collected from oystercatchers feeding on mussels using the stabbing feeding method. Intake rates are expressed as a percentage of those achieved in the absence of interference. Note that the Figure is plotted on logarithmic axes

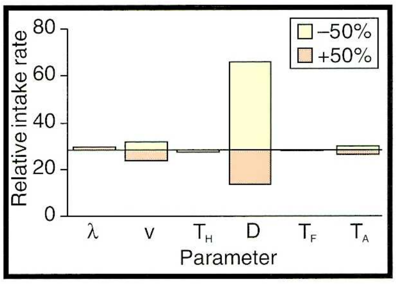

Figure 30. Sensitivity of the model predictions at high competitor density to changes in each parameter: prey encounter rate (λ), searching rate (v), handling time (T_H), encounter distance (D), duration of fights (T_F), and duration of avoidance (T_A). Each pair of bars shows the predicted intake rates at a density of 2000 birds ha^{-1} when a parameter value is either increased or decreased by 50%. All values are shown relative to that predicted using the standard set of parameters

stationary and involved in disputes over prey with another competitor. Animals differ in their dominance, with dominant individuals always defeating subdominants and winning the disputed prey item. Avoiding animals walk directly away from a competitor and are not able simultaneously to capture prey.

At the start of simulations, each animal is set to the searching state, positioned at a random location within the patch, and given a random searching direction. During each subsequent time interval, the model follows the location and behaviour of each animal as it moves around the patch and switches between behavioural states in the light of its encounters with prey and other competitors (Figure 28). Interference occurs in two ways: through lost searching time when an animal fights with or avoids another, and through lost prey when an animal is robbed.

The model was tested using data collected from oystercatchers (*Haematopus ostralegus*) feeding on mussels (*Mytilus edulis*) (Plate 11), based on the following provisional parameters estimates:

- prey encounter rate while searching (λ = 0.01 s^{-1})
- searching rate (v = 0.29 m s^{-1})
- handling time (T_H = 69 s)
- encounter distance within which animals interact (D = 2.5 m)
- duration of fights over prey (T_F = 6 s)
- delay after avoiding in which no prey can be captured (T_A = 2 s).

The predicted strength of interference was obtained by running simulations at a range of competitor densities, and tested against a separate field estimate of interference. Two sets of simulations were performed, one assuming that animals behaved in a fixed way when encountering others, as in existing theoretical models, and the other assuming that animals always adopted the behaviour which maximised their intake rate (Figure 29).

Comparison with the field data showed that both sets of simulations produced accurate predictions at low densities where little interference occurs. However, at high densities, the intake rates predicted when animals had a fixed response were far lower than that observed, whereas those based on an optimal response were much closer to reality. Too much interference occurred with a fixed response because dominant birds were wasting time avoiding subdominants and subdominants were wasting time attempting to steal prey from dominants, even though they always lost fights.

In contrast, with the optimal response, only subdominants avoided and dominants attacked so the overall intake rate was greater.

Incorporating an optimal response, therefore, substantially increased the accuracy of the model predictions at high densities. Although the optimal response produced a closer agreement with reality, the model still tended to overestimate interference at high densities.

To test which parameters may have been causing this discrepancy, a sensitivity analysis was run to determine the extent to which changes in parameter values influenced the model's predictions (Figure 30). This analysis clearly showed that the predicted strength of interference was most sensitive to changes in the distance over which encounters occurred, and highlighted that further refinement of this parameter could increase the accuracy of the model's predictions.

Although including only six parameters and a few simple assumptions, the model has shown promise in being able to predict with reasonable accuracy the strength of interference in a real predator/prey system. As the model is based on basic behaviour and optimality theory, it should produce reliable predictions under a wide range of circumstances. Future developments include detailed study of the nature of behavioural interactions in foraging shorebirds in order to add further realism to the model.

R A Stillman and J D Goss-Custard

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Plate 11. Oystercatcher (*Haematopus ostralegus*) feeding on mussels (*Mytilus edulis*)

Although including only a few simple assumptions, the model is able to predict accurately the strength of interference in a real predator/prey system.

surrounding landscape may arise through translocated species, causing:

- declines or extinctions of resident species through competition, predation, etc;
- changes in ecosystem or community processes;
- spread of pathogens and parasites;
- outbreeding depression of resident conspecifics;
- hybridisation with resident species (usually by non-native species).

Negative impacts may arise at and near the donor site (from which the translocated organisms originate – this is relevant to native species only) through:

- removal of individuals resulting in small population size;
- disruption of established metapopulations (especially following relocations);
- loss of relocated populations and communities.

Beneficial impacts (usually for native species only) include:

- establishment of new communities or of new populations of rare or regionally extinct species;
- rescue of populations or communities from destruction or extinction;
- habitat or community changes which enhance biodiversity;
- enhancement of metapopulations or provision of new habitat in the receptor landscape;
- increasing genetic variation of resident populations.

We reviewed a wide range of case histories of all types of translocations in the UK in order to determine their impacts on biodiversity (Bullock *et al.* 1995; Hodder, Bullock & Manchester 1996).

Plate 12. ITE is co-ordinating a project to re-introduce the large blue butterfly to the UK

Native species for conservation reasons

Such translocations are usually assessed only in terms of beneficial effects on biodiversity, ie the establishment or rescue of populations or communities; but metapopulations and genetics are rarely considered. Research has indicated that choice of an appropriate donor site is of prime importance and must also involve correct site preparation and management. For example, the large blue (Plate 12) requires specific conditions of a short sward and the presence of a particular host ant species. The method of translocation is also important; for example, habitat translocation by turfing may fail if the turves are kept out of the ground for too long. Other generic problems include the translocation of small numbers of individuals (leading to extinction through demographic stochasticity or inbreeding) and the use of maladapted genetic races (through captive breeding or use of non-local stock).

Although conservationists express disquiet about a number of possible negative effects on biodiversity, the

Research has indicated that choice of an appropriate donor site is of prime importance.

Table 9. Types of translocation of non-native species in the UK. All translocations are carried out for non-conservation reasons. All examples, apart from the biocontrol agents, are of species which are established in the wild in the UK, ie they have feral populations

Type of translocation	Examples of the introductions to the UK
Fish and shellfish for aquaculture and sport	Signal crayfish (*Pasifastacus lenuisculus*) Turkish crayfish (*Astacus leptodactylus*) Zander (*Stizedion lucioperca*) Rainbow trout (*Onchorhynchus mykiss*)
Biological control	Only in glasshouses, no classical biocontrol in the UK Coccinellid beetle (*Delphastus pusillus*) Predatory mite (*Amblyseius degenerans*) Mirid bug (*Macrolophus caliginosus*)
Wildfowl, game and for falconry	Red-legged partridge (*Alectoris rufa*) Pheasant (*Phasianus colchicus*) Rabbit (*Oryctolagus cuniculus*) American red-tailed hawk (*Buteo jamaicensis*)
Amenity and ornamental planting	Rhododendron (*Rhododendron ponticum*) Japanese knotweed (*Fallopia japonica*) Fuchsia (*Fuchsia magallanica*) Swamp stonecrop (*Crassula helmsii*)
Ornamental animals and pets	Goldfish (*Carassius auratus*) Canada goose (*Branta canadensis*) Sika deer (*Cervus nippon*) Grey squirrel (*Sciurus carolinensis*)
Forestry trees	Larch (*Larix decidua*) Norway spruce (*Picea abies*) Corsican pine (*Pinus nigra* var. *nigra*)
Accidental, ie brought accidentally to the UK, usually on ships	Cordgrass (*Spartina alterniflora*) Alga (*Sargassum muticum*) New Zealand flatworm (*Artioposthia triangulata*) Pacific cnidarian (*Haliplanella lineata*)
Others	
Crops	Oilseed rape (*Brassica napus oleifera*)
Fur animals	Mink (*Mustela vison*)


Plate 13. Dr Robert Kenward carrying out research on the introduced grey squirrel

basis of these concerns has been poorly studied. One subject attracting particular attention is the possible 'erosion' of genetic biodiversity by the use of non-local donor populations (eg re-stocking of otters (*Lutra lutra*) and the use of wildflower seed mixes). There has been no research to allow any assessment of this possibility.

Native and non-native species for non-conservation reasons

Biodiversity is rarely increased by non-conservation translocations, but declines in biodiversity are common. These declines are greater and more obvious than those caused by conservation translocations because the latter are more carefully planned and implemented. Causes of species decline or loss and community change are:

- competition, such as grey squirrels (*Sciurus carolinensis*) (Plate 13) replacing red squirrels (*Sciurus vulgaris*) and rhododendron (*Rhododendron ponticum*) invading heaths and woods;
- herbivory, such as coypu (*Myocaster coypus*) overgrazing reedswamp;
- predation, such as New Zealand flatworm (*Artioposthia triangulata*) on native earthworms and zander (*Stizedion lucioperca*) on other fish;
- disease and parasites, such as *Gyrodactylis salaris* spread with salmon (*Salmo salar*) and *Varroa jacobsoni* spread by bees.

There is some evidence that genetic mixing of commercially bred races of native species with wild populations may lead to outbreeding depression of the latter. This has been demonstrated for salmon, although it is not a problem for lobsters (*Homarus gammarus*). Hybridisation and introgression of non-native with native species has been demonstrated for sika deer (*Cervus nippon*) with red deer (*Cervus elaphus*).

Conclusions

Translocations have led to concern over their possible negative ecological effects and to interest in their beneficial uses for species and habitat conservation. As a result, new guidelines and legislation are being developed to control translocations. However, while some effects are well documented (eg negative effects of non-conservation translocations), others are poorly

Table 10 Practical measures of biodiversity which cover the full definition of biodiversity given by Hengeveld *et al* 1995 A decrease in any measure constitutes a decline in biodiversity

Single community
Species biodiversity
1 Number of characteristic[1] or priority[2] species
2 Population size of each characteristic or priority species
Genetic biodiversity
1 Amount of heritable genetic variation in each population of selected species
2 Genetic structure of each population of selected species[3]
Region
Species biodiversity
1 Number of characteristic (eg native) species
2 Number of priority species
3 Total number of individuals of each selected species
4 Number of populations of each selected species
5 Geographical range of each selected species
Genetic biodiversity
1 Total amount of genetic variation in each selected species
2 Amount of genetic difference among the populations of each selected species
3 Pattern of genetic differences among the populations of each selected species[3]
Landscape biodiversity
1 Area of each priority[4] landscape unit
The continuity of each priority landscape unit (ie the *lack* of fragmentation)

[1] Species characteristic to the community type
[2] Priority for conservation, eg rare or keystone species
[3] For this measure, a change, rather than a decline, indicates a decrease in biodiversity
[4] Priority for conservation, eg valley mire or Caledonian pinewoods have higher priority than improved grassland

New guidelines and legislation are being developed to control translocations.

researched (eg effect of population size on translocation success or consequences of using non-local genetic races in conservation translocations) Appropriate, structured monitoring and research are required to assess fully the effects on biodiversity and to inform policy- and decision-makers This will allow the development of techniques for the early detection and control of environmental problems caused by translocations and for improving the beneficial aspects of conservation translocations

Appropriate, structured monitoring and research are required to assess fully the effects on biodiversity and to inform policy- and decision-makers.

J M Bullock, K H Hodder and S J Manchester

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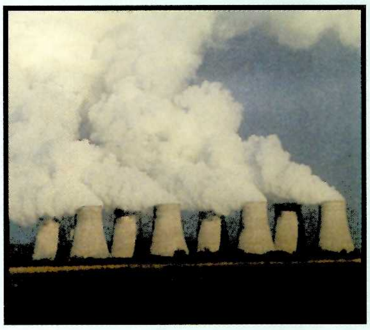
This represents the largest single programme of research following the restructuring of CEH science this year. Five main issues were identified:

- ***radionuclides***
- ***acidifying pollutants***
- ***photochemical oxidants***
- ***toxic metals***
- ***organic pollutants.***



In Press Photography

Pollution asssessment and control

The research is heavily influenced by increasing legislation, both national and international, for the control of chemical use, release and clean-up; this policy and regulatory orientation is underpinned with fundamental scientific research to understand mechanisms and derive models for the fate and effect of chemicals. The unifying theme behind all five issues is:

- hazard identification (the definition of dose causing adverse effects on organisms),
- risk assessment (quantitative estimation of degree of damage in the environment by comparing estimated exposure concentration with estimated effect concentration),
- risk management (the identification of ameliorative measures to reduce adverse effects).

Radionuclide research has modelled the fate and behaviour of isotopes in the environment both in the UK and the former Soviet Union. Factors affecting the uptake of radiocaesium, deposited following the Chernobyl accident ten years ago, have been determined for sheep grazing contaminated uplands in Britain. The article by Howard *et al.* describes the environmental and socio-economic factors which determine intake of radiocaesium in different human populations in the vicinity of Chernobyl. Both areas of work illustrate the importance of 'patchiness' in both bioavailability from the environment and uptake by individual animals of pollutant chemicals. Quantitative measures of factors affecting this patchiness have been derived by interdisciplinary studies looking at physicochemical mechanisms and the physiology of the organisms. The use of geographical information systems has improved the predictive value of the models. Ameliorative methods have also been studied to reduce uptake and effects of a range of radionuclides in both animals and humans.

Studies on acidifying pollutants continue to look at sulphur dioxide but are increasingly concentrated on nitrogen oxides and ammonia. Research is aimed at increasing understanding of atmospheric transformation, transport and deposition from the atmosphere, impacts on terrestrial organisms and communities, and the definition and mapping of critical loads Specific studies in this area are covered in the soils section of this Report

Increasing emphasis is being placed on damage caused to crops and natural vegetation by photochemical oxidants, the most important of which is ozone Collaborative work with university groups is described in the article by Ashenden *et al* The critical loads/levels approach, previously applied to acidifying pollutants, is now being used for ozone The article outlines the successful mapping of critical level exceedance for crops and forests in collaborative research However, as with other pollutants, there is considerable variability in response between species which has still to be described adequately An additional difficulty in deciding on the most sensitive component of ecosystems is the variability in the response of plants to temperature (frost sensitivity is increased following ozone exposure) and other environmental factors such as soil moisture A fundamental problem with pollution research in general has also emerged in this project the interaction of different chemicals in mixtures Attempts to predict the effects of ozone in combination with other atmospheric contaminants have shown that it is not simply additive

Interest in toxic metals in the environment has recently increased following a period of limited funding Recent research within ITE has looked at the effects of metal mixtures on plant growth and the modulation of those effects by soil properties, effects on mycorrhizal fungal communities, and inter-species differences in sensitivity to metals for small mammals, together with the influence of nutritional status on absorption Dose/response relationships between exposure level, uptake and effects of copper have been established for earthworms using both biomarker techniques and behavioural studies

Work continues on a range of organic pollutants, including the long-term monitoring of residues in wildlife Effects studies have included projects on wood preservative chemicals and bats, attempting to derive predictive tests without using bats in the laboratory The major thrust of new work on organics has concentrated on the fate and behaviour of chemicals in environmental media This work is aimed at improving the simple regulatory systems currently in place An example study is presented here in the article by Meharg One of the major outstanding questions in ecotoxicology is the bioavailability of chemicals present in soil and sediment Many compounds adsorb to inorganic and organic matrices which potentially reduces both uptake by organisms and breakdown by microbial metabolic processes The article demonstrates the importance of the microbiota, enhanced close to plant roots, in degrading an organic compound Macrobiota, such as earthworms, have also been shown to enhance the bioavailability and degradation of organics in soil The biological monitoring of exposure to chemicals has been studied using biomarker techniques which have correlated well with chemical analysis These findings have been used to estimate the degree and extent of contamination of the environment following release of chemical mixtures from industrial accidents As with other areas of pollution research, modelling plays an increasing role Fate models for organics are being developed in co-operation with other researchers

The major thrust of new work on organics has concentrated on the fate and behaviour of chemicals in environmental media.

This work is aimed at improving the regulatory systems currently in place.

S Dobson

ITE is participating in a research programme between the EC countries and Russia, Belarus and Ukraine on the consequences of the Chernobyl accident.

Ecological factors influencing the ingestion of radiocaesium by rural communities in Russia, Ukraine and Belarus

(This work was partly funded by the European Union)

For the last three years ITE has participated in a research programme between the EC countries and Russia, Belarus and Ukraine on the consequences of the Chernobyl accident. The programme, one of the Experimental Collaboration Projects (ECP), finished this year, coinciding with the tenth anniversary of the Chernobyl accident. The particular project in which ITE participated examined the comparative importance of different sources of radionuclides to rural communities living in contaminated territories (Plate 14).

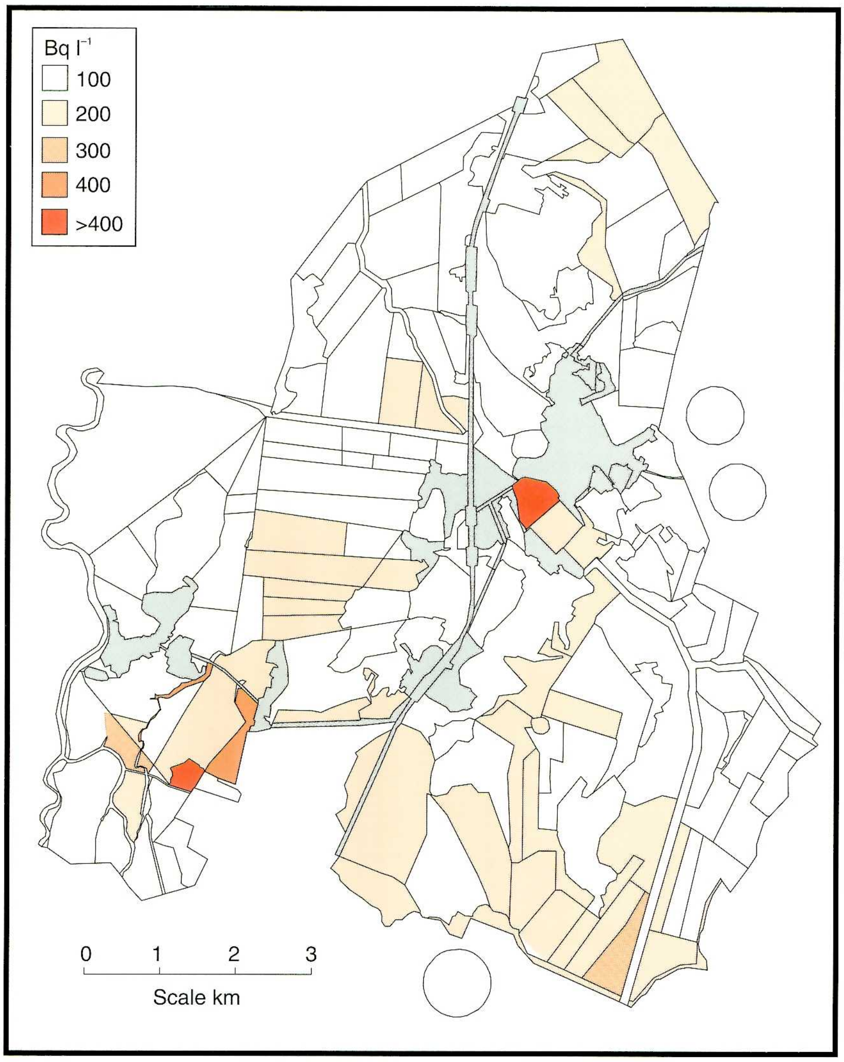


Figure 31. Predicted ^{137}Cs activity concentrations in milk for different fields in a contaminated study site in the Rovno region of the Ukraine

In regions contaminated by fallout from the nuclear accident at Chernobyl, the radiation dose received by the human population varies. Three study sites, one each from Russia, Ukraine and Belarus, were studied in depth with consolidation of existing datasets, field survey, whole-body measurements and questionnaires. The study examined a variety of factors influencing radiocaesium ingestion, including deposition, transfer from soil to vegetation and milk, the influence of countermeasures, and the diet of the local population.

Deposition

Information on the spatial distribution of deposition rates is crucial in dose assessment. Geostatistical techniques were applied at a landscape scale to identify not only the spatial variation in deposition, but also where there is the greatest uncertainty in current information (Luuriesma *et al.* 1995).

Soil types

The soil types in the contaminated areas determine rates of transfer to both plant and animal food products. High bioavailability of radiocaesium is associated with low amounts of clay minerals in organic soils and the high, but reversible, sorbing capacity of organic matter. Thus, ^{137}Cs retained in the upper organic horizon of highly organic forest and meadow soils is readily transferred to vegetation.

The three sites were dominated by podzolic soils, but in the Ukrainian site there were also extensive areas of peaty soils, which allow significant recycling of radiocaesium. Thus, although the deposition in this area was low compared to the other sites, the ^{137}Cs activity concentrations in foodstuffs was higher. Geostatistical analysis of time-series deposition data has shown that flooding can lead to increases in contamination levels (Burrough *et al.* 1996), suggesting a more dynamic system than previously thought.

Pathways

The availability of deposited radiocaesium for transfer to plants and animals is also dependent on the agricultural systems and land cover. The land cover in the study sites was agricultural land (mainly used by the collectives), unimproved meadows and forests. Surprisingly, the remaining problems of ^{137}Cs contamination are largely associated with the latter two categories.

Geographical information systems have been used to identify areas which are not suitable for supplying dairy cow fodder or as pasture for summer grazing. By combining information on deposition rates, soil types and transfer rates from soil to grass and milk, ITE constructed maps to show predicted milk ^{137}Cs activity concentrations in selected collective farm areas (Figure 31). Using this technique, pastures were identified which would give rise to milk with radiocaesium levels exceeding the EC intervention limit.

Radiocaesium activity concentrations in semi-natural foods have been much higher and more variable, both spatially and temporally, than those of agricultural products. The highest radiocaesium contents in semi-natural products have been recorded for various fungal fruiting bodies and for game animals, specifically roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*).

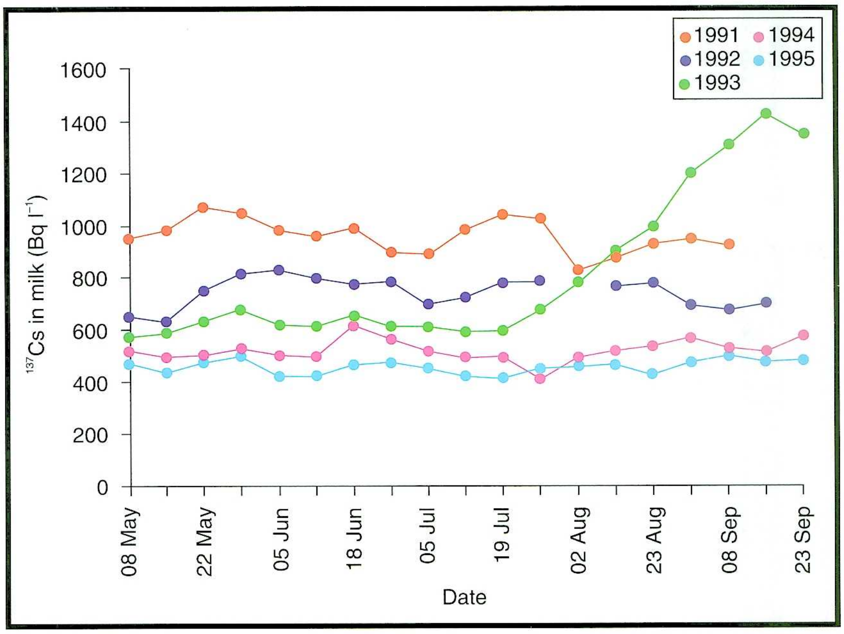


Figure 32. Changes with time in ^{137}Cs activity concentrations in bulk milk from cows grazing pasture in the Rovno region of the Ukraine (Strand, Howard & Averin 1996)

Changes with time

Radiocaesium levels in biota have generally decreased since the deposition of Chernobyl fallout, due to physical decay, weathering from surfaces, fixation in the soil, and the influence of countermeasures. The gradual fixation of radiocaesium in most soils normally leads to reduced bioavailability of radiocaesium over several years after an accident, until an equilibrium level is achieved. However, in semi-natural ecosystems, long ecological half-lives have been recorded for many species. For some game and mushroom species, the ecological half-life seems to be equivalent to the physical half-life for ^{137}Cs of 30.2 years. The long ecological half-lives in many semi-natural products compared with agricultural products means that the comparative importance of semi-natural products as sources of radiocaesium in the diet has increased with time.

In some circumstances, radiocaesium activity concentrations in food products increase. For instance, contamination of milk in the Ukrainian study site dramatically increased from 400–500 Bq l^{-1} to

Radiocaesium levels in biota have generally decreased since the accident, due to physical decay, soil fixation, and the influence of countermeasures.

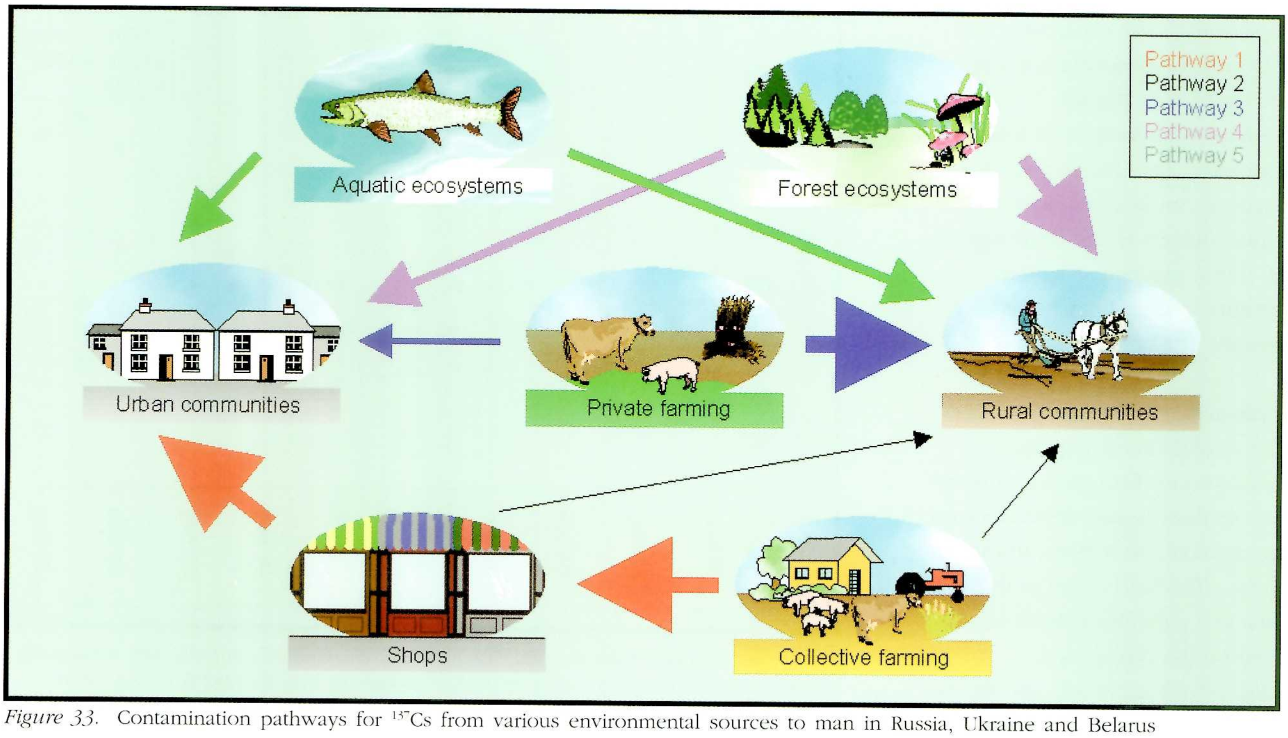


Figure 33. Contamination pathways for ^{137}Cs from various environmental sources to man in Russia, Ukraine and Belarus

The different pathways of contamination of food vary between population groups, depending on lifestyle and the extent of applied countermeasures.

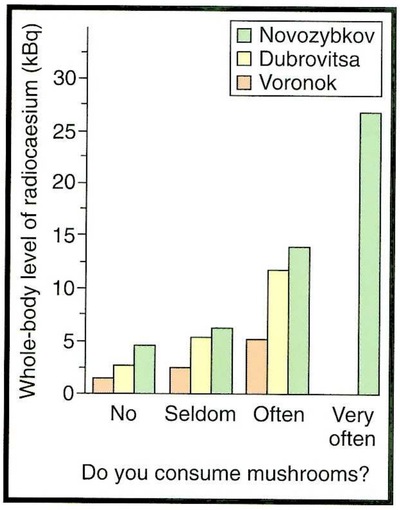


Figure 34. Influence of mushroom consumption on radiocaesium whole-body levels in residents of villages in contaminated areas (Strand *et al.* 1996)

over 1000 Bq l^{-1} as a result of the flooding of a peaty soil pasture in 1993 (Figure 32).

Comparative importance of different food sources

The different pathways of contamination of food vary between population groups, depending on lifestyle and the extent of applied countermeasures. Urban residents purchase food from shops which largely originates from the collective agricultural system, whereas much of the rural population are subsistence farmers who purchase few products from shops (Figure 33). As most countermeasures have been directed towards the collective system, the intake of radiocaesium via this route (pathways 1 and 2 in Figure 33) is currently low.

The contamination levels in foodstuffs grown by private farmers in rural areas (pathway 3 in Figure 33) will depend on many factors, including deposition rate, soil type and the extent of usage of forest areas. For rural inhabitants, the importance of the three different sources, collective farms, private farms and forests, varies considerably. However, food from private farms (largely milk, meat and potatoes) and forests contributes most of the total radiocaesium intake. Furthermore, dietary questionnaires and whole-body monitoring by our Norwegian, Russian and Ukrainian colleagues has shown a clear correlation between the consumption rate of mushrooms and the whole-body radiocaesium content of rural inhabitants (Figure 34).

Remediation

Rapid and effective intervention in collective agricultural environments has ensured that the vast majority of collective produce has radiocaesium levels which are well below intervention limits.

A wide range of effective agricultural and household treatments are available to reduce contamination, but their effectiveness varies according to application technique and local conditions. Soil treatment to reduce radionuclide uptake by plants has been, and continues to be, among the most important and extensively used remediation measures after the Chernobyl accident.

Despite the wide range of currently available remediation measures, there are problems even ten years after the Chernobyl accident:

- ^{137}Cs contamination of private milk in certain regions
- ^{137}Cs intake via semi-natural products, especially mushrooms, where intervention limits are substantially exceeded
- transitory increases in contamination levels due to seasonal or flooding events.

Some of these problems arise because the currently available countermeasures cannot be used successfully. It is apparent that the usefulness of remediation measures needs to be considered with regard to many factors, including not just effectiveness but also cost, ease of use, local availability and social acceptability. Overall, an important final consideration is whether they will be used by the target community. In the case of milk from private farms, it is therefore important to consider the views and attitudes of private farmers.

Conclusions

Possible remedial measures, appropriate to private farms, need to be evaluated further so that ^{137}Cs activity concentration in their milk output can be reduced below intervention limits. Further information on the importance of mushroom consumption in both rural and urban communities is required to allow appropriate measures to be taken. There is a need for integrated environmental management after the Chernobyl accident because remaining problems will best be solved by an interdisciplinary approach which considers the chemical, biological, agricultural and social aspects of each issue.

Plate 14. Ukrainian colleagues sampling private vegetables for ECP9

Acknowledgments

This review is based on results achieved within the European Union Project ECP9 and, therefore, the contribution of all participants in this programme is gratefully acknowledged.

B J Howard, M K Gillespie, D C Howard and A S Culling

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There is a need for integrated environmental management after the Chernobyl accident.

Plate 15. Heather plants after a natural frosting event following exposure to 70 nl l^{-1} ozone or charcoal-filtered air (control)

Physiological and growth studies effects on plants to underpin critical levels for ozone

There has been increasing interest in the effects of ozone over the last year as international discussions on the control of emissions of oxides of nitrogen have focused upon the effects of tropospheric ozone on vegetation. Ozone is produced by the action of sunlight upon mixtures of nitrogen oxides and volatile organic compounds (VOCs), so reducing the harmful effects of ozone has implications for both of these groups of pollutants.

The critical level of ozone is considered as the threshold concentration or dose above which harmful effects may occur. International discussions are aimed at reducing pollutant levels below the critical level, but for this a good scientific understanding of the threshold is required. Work in ITE is addressing the problem and seeks:

- to estimate the critical level for ozone of a range of plant species,
- to identify those areas where the critical level may be exceeded, and
- to estimate the type of damage which may result from excess concentrations.

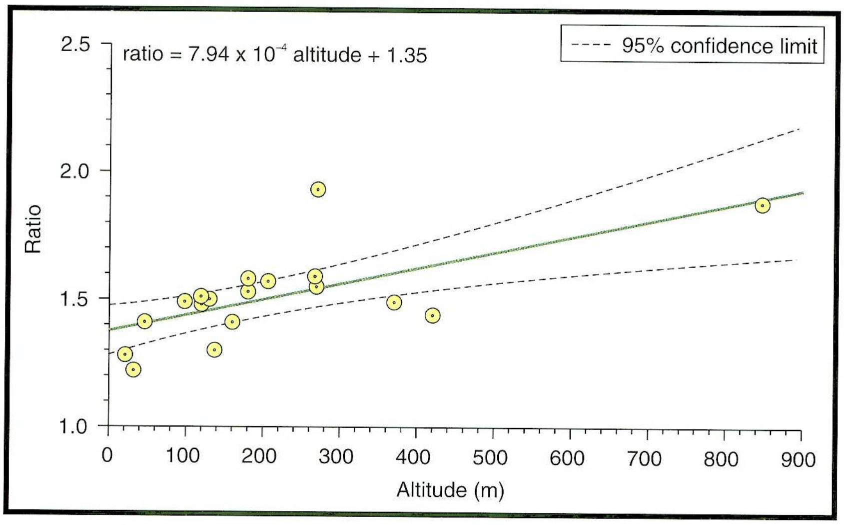

Figure 35. The relationship between altitude of monitoring station and the ratio of daytime AOT40/AOT40 for the period 1200–1800

In 1993, an international workshop in Berne, held under the auspices of the United Nations Economic Comission for Europe (UN-ECE) Convention on Long Range Transboundary Air Pollution, defined critical levels for cereal crops and forest trees (Fuhrer & Achermann 1994). These critical levels have been applied for UK calculations and the results are summarised below. More recently, another international workshop under the Convention, held in Kuopio, Finland (Kärenlampi & Skärby 1996), considered the latest experimental data and agreed threshold doses (critical levels) of ozone for crops, trees and natural vegetation. Those for crops and trees are similar to those agreed at Berne, although UK estimates are to be revised in line with the workshop recommendations. The implications of the ozone critical levels for UK natural vegetation are considered below.

Cereal cropland

The 1993 workshop identified critical levels of ozone for cereals (Fuhrer & Achermann 1994). The workshop concluded that the accumulated exposure over a threshold of 40 ppb (AOT40) should be set at 5300 ppbh. ITE has mapped the areas exceeding this value.

The monitoring networks for ambient O_3 in the UK include a rural network of 17 stations distributed throughout the country; they are described in detail by the Photochemical Oxidants Review Group (PORG 1994) with appropriate data summaries for the period 1986–92. This network is too sparse simply to interpolate between stations from the AOT40 statistics for individual stations. The systematic effects of altitude may introduce misleading trends in the extrapolation of O_3 exposure.

To map the AOT40 value for daylight hours, it is necessary to quantify the degree to which an individual grid square (mapping at 1 km x 1 km resolution) is coupled with the boundary layer ozone concentrations. This may be quantified using the ratio of the AOT40 for the full daylight period (defined arbitrarily as the period between 1 h after sunrise and 1 h before sunset), and the AOT40 for the period of the day with a well-mixed boundary layer from which the base map was interpolated. This ratio when plotted against altitude is approximately linear (Figure 35), with the largest ratio at high-altitude sites (sites which have the smallest diurnal range in concentration). A map of mean altitude for each 1 km x 1 k m grid square then enables the relationship from Figure 35 to be used to construct an AOT40 map for the entire country (Figure 36). The areas exceeding the AOT40 include most of the wheat-growing areas in southern and central England but also substantial areas of the uplands and the north where wheat is not grown.

Forest

For the assessment of the critical level for forests, rather different criteria were agreed at the Berne workshop. The experimental evidence, although less robust than that for wheat or field beans, supported a similar threshold of 40 ppbV. In view of evidence of night-time O_3 uptake, an exposure period of 24 h was accepted. An AOT40 for forests of 10^4 ppbh calculated for 24-h exposure and a six-month growing season was set at the Berne workshop, based on a 10% reduction in plant biomass (Fuhrer & Achermann 1994). The relationship between the ratio of AOT40 for the 24 h to that for the period 1200–1800 (Figure 37) allows the 1 km x 1 km resolution map of AOT40 for forest to be constructed (Figure 38) from the relationship between altitude and the ratio AOT40 for the 24 h/AOT40 for 1200–1800 GMT.

A map of forest cover in each 1 km x 1 km grid square may then be overlain with the 1 km x 1 km AOT40 map for forest to assess exceedance and the proportion of UK grid squares (and forest) which are currently subject to O_3 exposure above the critical levels. Maps show that 35% of the UK 1 km^2 grid squares exceed critical levels for forest, and that the forest areas within these grid squares represent 46.8% of UK forest, largely in southern England and Wales but including large plantation forests in Northumberland and the Scottish Borders.

Native vegetation

A recent international workshop in Finland (Kärenlampi & Skärby 1996) considered the latest experimental data and agreed, for the first time, a critical level of ozone for natural vegetation. However, many uncertainties still remain because of a lack of research on native species as opposed to crop plants. A priority in the derivation of meaningful critical levels for native ecosystems is the determination of the relative

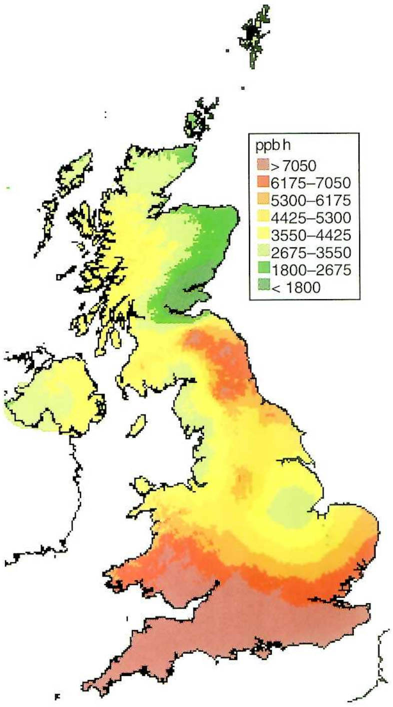

Figure 36. The UK AOT40 ozone exposure map for wheat for three months (May–July) in daylight hours

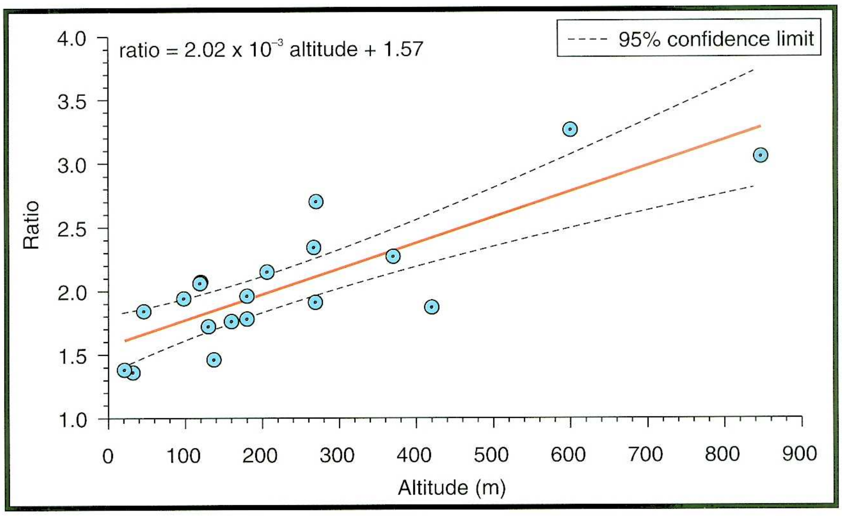

Figure 37. The relationship between altitude of monitoring station and the ratio of 24 h AOT40/AOT40 for the period 1200–1800

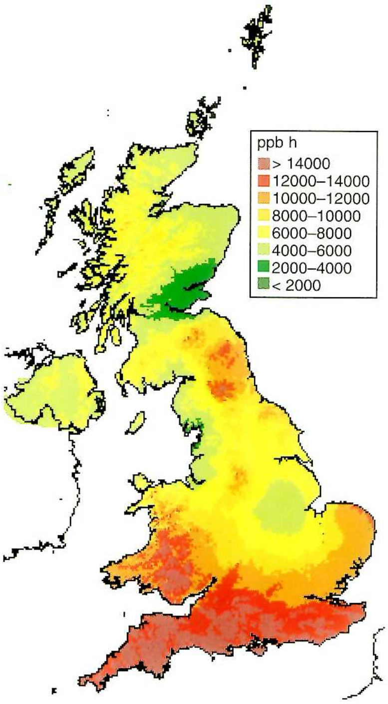

Figure 38. The UK AOT40 ozone exposure map for forest for six months (April–September)

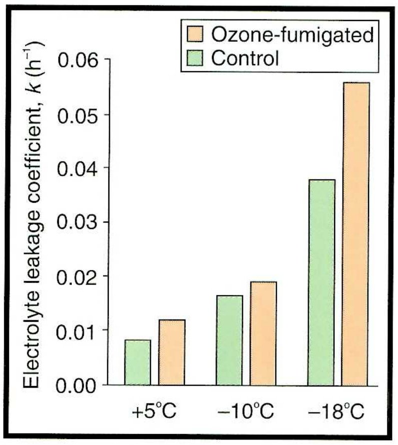

Figure 39. Relative rates of electrolyte leakage following controlled frosting regimes for heather shoots exposed to charcoal-filtered air (control) or 70 nl l^{-1} O, 8 h d^{-1}, 3 d week^{-1} (ozone) (Foot *et al.* 1996)

sensitivities of component species. To date, a comparative study of only a small number of species has shown a broad range of responses to ozone (Reiling & Davison 1992a), and there is a large ecotypic variation within species (Reiling & Davison 1992b). Collaborative research between ITE Bangor and the University of Newcastle upon Tyne has shown that, even between ecotypes with different ozone sensitivities, there is a complex suite of responses that vary both with the population and level of ozone exposure (Pearson *et al.* 1996).

Further complications in defining critical levels are that species sensitivities to ozone may vary depending on other environmental factors. We have shown that the effects of ozone in pollutant mixtures are not necessarily additions of the effects on plants of singly applied pollutants (Ashenden, Bell & Rafarel 1996). Temperature may also affect the sensitivity of plants to ozone. In a collaborative study with the Universities of Sheffield and Manchester Metropolitan, plants of heather (*Calluna vulgaris*) were found to be more sensitive to ozone during winter as opposed to summer exposure periods (Foot *et al.* 1996).

In addition to direct effects on plant growth, exposure to ozone increased the susceptibility of heather to frost injury. Shoots from control and ozone-fumigated plants were subjected to 3-h, controlled, artificial chilling treatments of +5°C, −10°C and −18°C. Measurements of relative electrolyte leakage, an established technique for assessing frost injury, revealed significantly greater damage ($P \leq 0.001$) to ozone-treated plants (Figure 39). Further evidence for this conclusion was obtained following an unplanned, naturally occurring period of sub-zero temperatures in the open-top chambers at ITE Bangor in December 1995. Visual scoring of plant injury revealed that 29% of plants in ozone-fumigated chambers, as compared to none in control chambers, had suffered more than 50% damage (browning/death) to shoots (Plate 15). The mean length of damage sustained by individual shoots was 10.2 cm and 2.3 cm, in plants exposed to ozone and charcoal-filtered air, respectively. An increased sensitivity to ozone at low temperatures and reduced frost resistance have important implications for upland heather heathlands. Changes in the canopy structure of heather may allow more aggressive and less ozone-sensitive species to colonise and result in the gradual loss of this species from upland ecosystems in the UK.

Conclusions

Much more research is required in order to refine our estimates of critical levels of ozone, particularly for native vegetation. More detailed assessments need to be made of the range of sensitivities both between and within species and the potential interactive effects of other environmental variables and management factors, such as grazing regimes, on plant susceptibility to ozone.

The critical levels and the areas where they are exceeded have been used for an initial assessment of impacts for the UK. Revised calculations are being made for the new critical levels agreed at the Kuopio workshop. At this workshop it was also agreed that the simple critical levels based upon AOT40 values were not sufficient in themselves to quantify the extent of damage. Other factors, such as soil moisture, must be taken into account to define the extent and magnitude of damage to crops and trees.

Further work is continuing in ITE in order to calculate these factors and thus provide quantitative estimates of damage by ozone across the UK.

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Breakdown of xenobiotics in the rhizosphere

The main environmental reservoir of organic xenobiotics (PAHs, PCBs, dioxins, organochlorine pesticides and substituted benzenes, amongst others) in the terrestrial environment is in the topsoil. A wide range of studies have shown that xenobiotics are highly persistent in soils because of slow degradation and their low bioavailabilty (due to high affinity for the soil matrix). However, these studies rarely consider the interactions that soil macrobiota have on fate in soil. For instance, a recent study has shown that the presence of earthworms alters the

Macrobiota affect the fate of organic chemicals in soil.

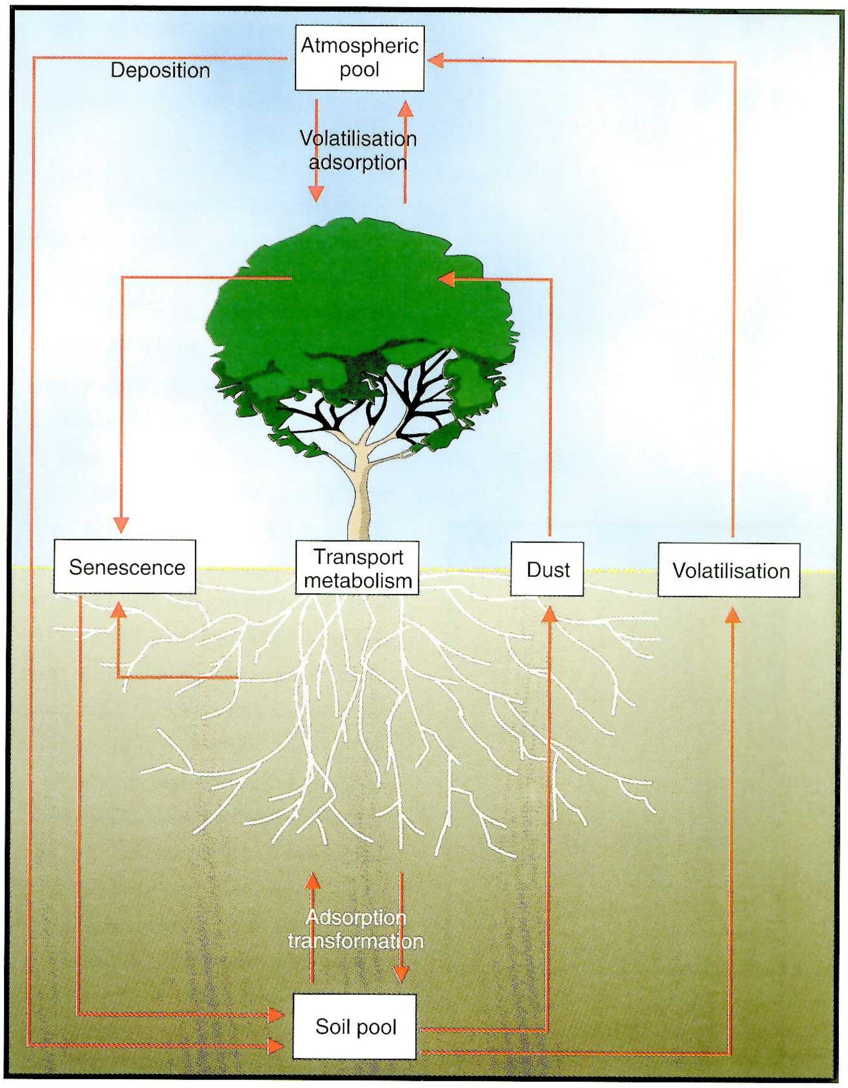

Figure 40. Xenobiotic cycling within plant/air/soil systems

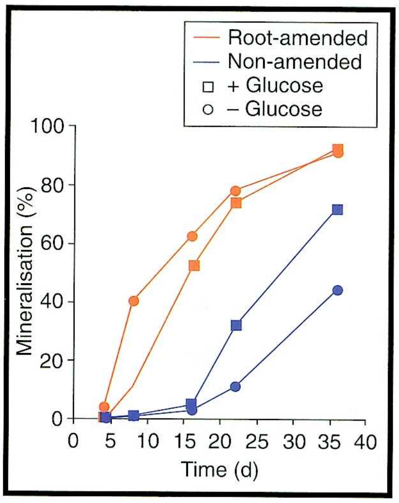

Figure 41. Mineralisation of MCB in root-amended and in non-amended soils in the presence of glucose and in the absence of glucose. Each point is the average of three replicates

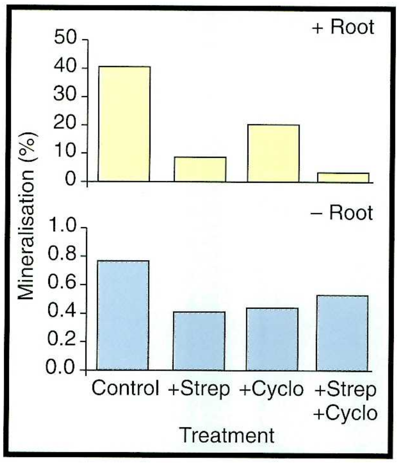

Figure 42. Mineralisation of MCB after 4 d incubation in the presence and absence of roots and in the presence and absence of microbial inhibitors. Each point is the average of three replicates

bioavailability and degradation of atrazine in soil (Meharg 1996). Plant roots may also alter the degradation and cycling of xenobiotics in soil, as outlined in Figure 40.

There is increasing evidence that the rhizosphere is a zone of increased degradation of persistent organic pollutants (Anderson, Guthrie & Walton 1993). The enhanced rates of degradation of organics observed in the rhizosphere are thought to be due to the increased size and activity of the rhizosphere microbial biomass compared to bulk soil. However, other factors such as selection in the rhizosphere of organisms capable of utilising complex plant-derived material may also explain enhanced degradation rates. Micro-organisms in the rhizosphere normally utilise natural aryl compounds, and hence may degrade pollutants containing aryl rings.

Experimental approach

To investigate the factors controlling the degradation of aromatic compounds, the fate of monochlorobenzene (MCB) in the presence and absence of roots was investigated. MCB is a common environmental contaminant as it is widely used as a solvent and chemical feedstock in a range of industrial applications. To investigate factors controlling the fate of MCB, uniformly labelled ^{14}C MCB was added to an agricultural soil in the presence and absence of plant roots and in the presence and absence of a readily utilisable carbon source (glucose). Glucose was added to determine if any enhanced degradation in the presence of roots was due to the enhanced size and activity of the microbial biomass caused by increased carbon supply in the rhizosphere. Mineralisation, loss of parent compound, and incorporation of label into degradation products were determined, although only the results of ultimate degradation (mineralisation) are presented here. Specific inhibitors of fungi and bacteria were used to investigate which components of the microbial biomass were capable of degrading MCB.

Effects of plant roots on degradation

Mineralisation of MCB was greatly enhanced in the presence of plant roots of the grass Yorkshire-fog (*Holcus lanatus*) (Figure 41). In the presence of roots there appeared to be no lag phase in mineralisation, whereas a distinct lag phase was observed in the absence of roots. Mineralisation in the root-alone treatment was extremely rapid, with 40% of the added label mineralised after eight days and over 90% after 37 days. Addition of glucose when roots were also present substantially inhibited mineralisation at the early stages of the incubation (Figure 41). However, by the termination of the experiment, both root treatments had mineralised equivalent amounts of the label. In the absence of roots there was a lag phase in mineralisation which lasted for 16 days when mineralisation increased considerably, both in the presence and absence of glucose (Figure 41). The presence of glucose in the absence of roots stimulated mineralisation in comparison to the unamended control once the lag phase in mineralisation had passed. The glucose-amended treatment mineralised about 70% of the label compared to 40% for the unamended treatment at the termination of the experiment.

Microbial aspects of degradation

The use of selective inhibitors of bacterial and fungal biomass showed that, while both inhibitors caused significant declines in mineralisation after four days of incubation, the bacterial inhibitor (streptomycin sulphate) was more effective at inhibiting mineralisation than the fungal inhibitor (cycloheximide) (Figure 42). The effectiveness of the inhibitors after four days of incubation may be questionable (as there might be adaptation to the inhibitors or resistant strains may proliferate). However, any substantial decrease in mineralisation will indicate that the inhibitors were, at least, partially effective. Both inhibitors substantially decreased mineralisation, showing that both the fungal and bacterial biomass were capable of degrading MCB. The combined effect of the two inhibitors on mineralisation in the presence of roots was considerable, indicating that the inhibitors were working effectively (Figure 42). In the absence of roots, the mineralisation rate observed after four days was very low and all inhibitor combinations only reduced mineralisation by about 50% (Figure 42).

Presence of roots in this soil increased the size of the bacterial biomass by up to 2.5-fold and the active fungal biomass by up to 5-fold, as determined by viable staining (DNA staining for bacteria and fluorescein diacetate staining for fungi) followed by enumeration by fluorescence microscopy (Figure 43). Bacterial numbers remained fairly consistent for both treatments, while the active fungal biomass was more dynamic. In the absence of roots the fungal biomass increased with time, while in the presence of roots the fungal biomass declined from about 50% and then recovered to its original level by 56 d. The large increase in biomass observed from 28 d to 56 d was also observed in the 'minus-root' treatment.

Conclusions

In conclusion, enhanced mineralisation of MCB occurred in the presence of roots which appeared to be due, at least, to the increased size of the microbial biomass. Glucose addition to soil was less effective at stimulating mineralisation compared to plant roots alone, suggesting that enhanced mineralisation was not solely caused by increased carbon supply in the rhizosphere. Both bacterial and fungal communities contributed to mineralisation of MCB in the rhizosphere. These results indicate that there is a considerable potential for using rhizospheres to enhance the degradation of aromatic pollutants in soils.

A Meharg

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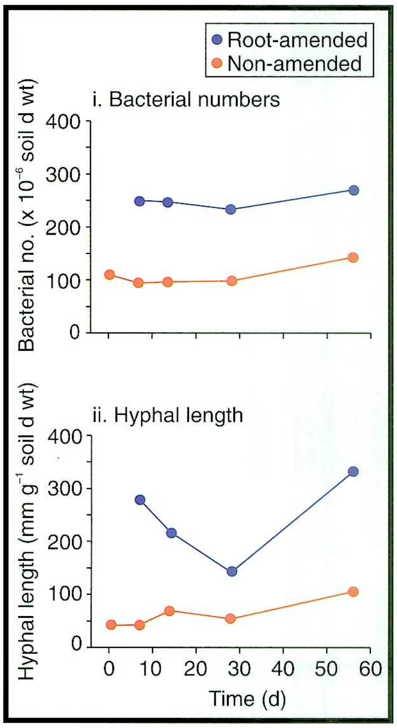

Figure 43. (i) Vital bacterial counts and (ii) vital fungal hyphal length in root-amended and non-amended soil. Each point is the average of three replicates

The presence of plant roots enhances the mineralisation of monochlorobenzene.